Collective turns in jackdaw flocks: kinematics and information transfer

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Abstract: The rapid, cohesive turns of bird flocks are one of the most vivid examples of collective behaviour in nature, and have attracted much research. 3D imaging techniques now allow us to characterise the kinematics of turning and their group-level consequences in precise detail. We measured the kinematics of flocks of wild jackdaws executing collective turns in two contexts: during transit to roosts and anti-predator mobbing. All flocks reduced their speed during turns, likely due to constraints on individual flight capability. Turn rates increased with the angle of the turn so that the time to complete turns remained constant. We also find that context may alter where turns are initiated in the flocks: for transit flocks in the absence of predators, initiators were located throughout the flocks, but for mobbing flocks with a fixed ground-based predator, they were always located at the front. Moreover, in some transit flocks, initiators were far apart from each other, potentially due to the existence of subgroups and variation in individual interaction ranges. Finally, we find that as the group size increased, the information transfer speed initially increased, but rapidly saturated to a constant value. Our results highlight previously unrecognized complexity in turning kinematics and information transfer in social animals.

Key words: collective behaviour; bird flocks; collective turns; flight kinematics; information transfer; 3D imaging;

Introduction

Collective behaviour is observed for a broad range of biological systems, from cell colonies [1], insect swarms [2,3], fish schools [4,5], and groups of mammals [6–8], including human crowds [9]. One of the most spectacular illustrations of collective behaviour occurs when whole groups of hundreds of individuals suddenly change direction, executing cohesive turns like a single, cohesive unit [10,11]. These collective turns may be triggered by local changes in traveling direction [12,13], external stimuli such as predator attacks [14–16], or may simply be stochastic, spontaneous effects [17–20]. Usually, a few individuals are observed to turn first and are subsequently followed by other group members [16,20,21], causing shimmering waves to propagate rapidly through the entire group [14,22]. Such synchronization among group members during collective turns is crucial for maintaining group cohesion and thus for the survival of group-living animals [23,24]. Understanding the mechanisms responsible for collective turns and information transfer among group members therefore has significant ecological and evolutionary implications [25,26].

Bird flocks are one of the most extensively studied examples of collective behaviour. Following the development of seminal mathematical models of self-organising systems [27–29], collective behaviour is typically thought to arise as an emergent property of local interactions between individuals [11,30]. Consequently, many studies have focused on inferring the interaction rules followed by birds [31–40] and their implications for macroscopic quantities such as flock morphology [32,38,41] and the spatial distance over which the velocity fluctuations of individuals are correlated [37,42,43]. Flocking behaviour, including collective turns, has also been numerically simulated using discrete self-propelled particles

[44,45], network models [46], and continuum hydrodynamic models [47,48]. Although there have been a number of empirical studies on the collective turns of large groups of birds in the wild [14,18,21,49,50], many questions remain outstanding. In particular, the turning kinematics such as flight speed and radial acceleration have not been well characterized. Since these quantities are constrained by the flight capabilities of individuals, they offer a potential connection between individual- and group-level properties. It is also unclear how group size affects the speed of information propagation within the group.

The simplest way to characterize collective turns is to quantify the kinematics of each involved individual. In this vein, the temporal variation of radial acceleration and group polarization during turns has been reported for starling flocks [21]. However, many other relevant kinematic quantities such as flight speed, turn rate (i.e., angular velocity), turn radius, and angular momentum have not been studied. Individual group members slowing their movement speed have been shown to trigger collective turns in fish schools [20,51], and so studying the temporal variation of flight speed can help to test whether flocking birds use a similar mechanism. Moreover, evading predators depends on how quickly a flock can adjust its flight direction, suggesting that one should measure a flock's turn rate and its relationship with the magnitude of the change of traveling direction θ_g (where θ_g=180 degrees for a U-turn). Examining the radial acceleration allows us to test whether the centripetal forces produced by birds are constrained by inherent biophysical limitations [52,53]. An upper limit on the radial acceleration could explain why movement speed is reduced during turns [20]. Thus, fully characterizing the kinematics of collective turns is essential to better understand how avian flocks execute these coordinated manoeuvres.

Studying the distribution of spatial locations from which turns can be initiated can also reveal aspects of how information flows through the group. In small flocks of pigeons (<10 individuals), it was found that birds at the front of the flocks were most likely to start the turns [12]. In very large starling flocks (>100 individuals), however, the first birds that started to turn were found to be located close to each other [21], but tended to be on the sides (in elongated tips) of the flocks rather than at the front [18]. In contrast, in fish, individuals located in the rear part of a school can also initiate turns [20]. Since birds have a wide field of vision and often produce vocalisations while flocking, turns may also plausibly be initiated from the rear of the flocks. In addition, given that flocks of some species contain multiple subgroups [38,54,55] and that some individuals may have longer interaction ranges (either interacting with more neighbours or having a longer range of perception) than others [37,56–58], the first birds that start to turn may not always be close to each other. New observational data are required to address these questions. Moreover, since predators may attack flocks from any directions, testing whether birds located at various positions in flocks have the ability to initiate collective turns is central to understanding the adaptive function of collective turning as a predator avoidance strategy.

Finally, only a few empirical studies [21] have investigated how group size affects information transfer in bird flocks. Given evidence that larger groups make faster and more accurate decisions than smaller groups [59], it is likely that group size has a strong influence on the speed of information transfer through flocks. For instance, research on fish schools has shown that the information transfer speed (i.e., the speed with which information about a turn propagates within the group) increases as the group size grows from 2 to 20 individuals [20]. However, for birds, researchers have found that there is no correlation between group size and information transfer speed for starling flocks with sizes ranging from 50 to 595 [21]. Determining whether the different results for these cases stems from the difference in species or a group size effect requires data for flocks with sizes in the range of 10 to 50 individuals.

In this study, we address these open questions by tracking the three-dimensional (3D) motion of flocking jackdaws (*Corvus monedula*), a small member of the large-brained corvid family. Jackdaws form flocks with group sizes ranging from two to several thousand [38,60]. Their flight paths and roosting sites are predictable, allowing for data collection using a ground-based 3D imaging system [61]. We study collective turns made by flocks with a range of sizes, in the absence of real predators but under two

different ecological contexts. We describe the turning kinematics including flight speed, turn rate, turn radius, radial acceleration, all as functions of θ_g. We also show that the first birds that start to turn can be located variously in the rear or front of the flocks, and can be either close to or far apart from each other. Finally, we find that group size does indeed affect the information transfer speed, particularly for smaller groups.

Materials and Methods

(*a*) *Study species*

Jackdaws (*Corvus monedula*) are a highly social, colony-breeding corvid found throughout much of the Western Palaearctic. At our study sites in Cornwall, UK, more than 2000 jackdaws are fitted with unique colour ring combinations for individual identification. We study collective turns in two types of flocks: transit flocks and mobbing flocks. In the winter, jackdaws gather in large flocks around pre-roost and roost trees before they spend the night at the roost sites. These pre-roost and roost sites are predictable and consistent, allowing for observations of the transit flights of flocks between them. During the breeding season, jackdaws also form mobbing flocks in the vicinity of their nest-boxes aimed at driving away aerial and terrestrial predators such as raptors and foxes. During this time period (May to July), jackdaws can be readily recruited into mobbing flocks by pairing presentations of a model predator (a taxidermy fox) with playbacks of pre-recorded anti-predator recruitment calls (known as scolding calls) [62], facilitating data collection (see details in *electronic supplementary material*). Both transit and mobbing flocks provide excellent opportunities to study how social birds make collective turns and how information spreads through flocks.

There are two essential differences between transit and mobbing flocks. Transit flocks contain pairwise subgroups that are attributable to the life-long monogamous pair bonds in jackdaw societies [37,63,64], as well as larger clusters of birds flying together (potentially reflecting groups from different colonies joining together within large flocks) [38]. In contrast, mobbing flocks formed in response to experimental presentations of scolding calls and model predators during the breeding season do not contain such internal sub-structure (see details in *electronic supplementary material*). Additionally, the collective turns in transit flocks mostly arise from a stochastic change of traveling direction, while in mobbing flocks they are responses to spatially localized scolding calls and predators. In transit flocks, we cannot exclude the possibility that external stimuli such as wind or other flocks outside our imaging volume could also play a role in triggering turns. We will show below that these two types of flocks have different turning behaviour: the locations from which turns are initiated in mobbing flocks are always in front of the flocks, while those in transit flocks can be anywhere in the flocks.

(b) *Data collection*

Using a multi-camera three-dimensional (3D) imaging system [61] (see *electronic supplementary material*), we recorded 21 flocking events consisting of 4 to 197 jackdaws (Table 1). 13 events were collected during the winter season near pre-roost sites at Mabe and Gwennap, Cornwall, and 8 events during the breeding season near nest-box colonies near Stithians, Cornwall (see *electronic supplementary material* for more details of the data collection procedures). Each event was captured at 60 frames per second for a time period long enough for flocks to complete a single turn. The event selection criteria included: (i) the flock changed its traveling direction by more than 90 degrees; (ii) the group size N (i.e., the number of birds in the flock) was larger than 4; (iii) flock images were captured by all four cameras; (iv) all birds were jackdaws (identified by vocalisations and morphological characteristics) to avoid any effects caused by species differences [63]; and (v) no real predators were present.

From the recorded images, we reconstructed the 3D trajectories of individual birds within the flocks. First, we determined the 2D intensity-weighted centroids of each bird on each image. We matched these 2D coordinates across all four cameras by finding candidates located within a small tolerance of the epipolar lines. The matched candidates were combined to calculate 3D locations using a least-squares

solution of the line-of-sight equations [65]. When multiple 3D positions for the same bird were possible, we selected the one with the smallest 3D ray intersection distance (that is, the residual of the least-squares solution). We solved the optical occlusion problem by associating every detected bird on each camera with a 3D position [61].

We linked the 3D locations belonging to the same bird over time based on a three-frame predictive particle tracking algorithm [66]. We applied a Gaussian smoothing and differentiating kernel [67] to the 3D trajectories to obtain accurate velocities and accelerations. Wingbeat-induced noise was removed by applying a low-pass filter to the measured acceleration [61]. For every time step t, we measured the position $\boldsymbol{x}=(x_1, x_2, x_3)$, velocity $\boldsymbol{u}=(u_1, u_2, u_3)$, and acceleration $\boldsymbol{a}=(a_1, a_2, a_3)$ of individual birds in a Cartesian coordinate system. We aligned $-x_3$ to the gravity direction and $+x_1$ to the mean traveling direction of all birds in the flock at t=0 before a turn was initiated.

(*d*) *Bird ranking and turning delay*

We ranked birds from the first to turn to the last to turn, assigning a rank index r_i ranging from 1 to N to each bird. To do so, we followed the method used by Attanasi *et al.* (2014) [21]. First, we calculated the time lag τ_{ij} (in the manner discussed below) between each pair of birds i and j, where $\tau_{ij}>0$ means that bird i turns earlier than bird j. Then, we assigned a score $w_{ij}=1$ if $\tau_{ij}<0$ (or $w_{ij}=-1$ if $\tau_{ij}>0$) for bird i. After considering all pairs, the total score for bird i was calculated as $W_i=\sum_{j\neq i} w_{ij}$, where a smaller W_i means that bird i turns earlier than a larger number of other birds in the group. Therefore, we can define r_i based on W_i, since a smaller W_i corresponds to a smaller r_i.

To calculate τ_{ij}, we used the correlations of the velocity, defined as $C(\delta t)=\langle \boldsymbol{u}^i(t)\cdot\boldsymbol{u}^j(t+\delta t)\rangle_t/\langle|\boldsymbol{u}^i|\cdot|\boldsymbol{u}^j|\rangle_t$, where $\boldsymbol{u}^i$ and $\boldsymbol{u}^j$ are the velocities of birds i and j respectively, $\langle\ \rangle_t$ represents a time average, and δt is a time shift. τ_{ij} was chosen as the time when C reached its maximal value. We use correlations of the velocity instead of the radial acceleration to measure τ_{ij}, since the velocity signal is less noisy than the acceleration signal.

After ranking the birds, we calculated the turning delay t_i for each bird, i.e., the time when the bird starts to turn. Still following [21], for the bird with rank r_i=1, we set t_i=0, and for birds with rank r_i>1, $t_i=\sum_{rj<ri}(t_j+\tau_{ij})/(r_i-1)$. According to [21], this method is a robust estimate of the turning delay even under some time-ordering violations $\tau_{ij}\neq\tau_{ik}+\tau_{kj}$. Based on the locations of birds with r_i=1 and t_i=0 within the flocks, we then know where a turn is started. By investigating the spatial distribution of t_i, we can study how information about the turn propagates through the flock.

Results

(*a*) *Turning kinematics*

A sample collective turn made by a mobbing flock consisting of N=70 birds is illustrated in Fig. 1(a). Flight trajectories and speeds of three birds with r_i=1, N/2, and N are shown in Fig. 1(b) and (c). For $0<t<1$ s, the flock is highly polarized as all birds move in nearly the same direction. For $1<t<2$ s, a small number of birds located in the front of the flock slow down and begin to turn backwards, while the other flock members keep moving in the same direction. For $2<t<4$ s, birds in the middle of the flock begin to slow down and turn backwards, followed finally by birds in the rear of the flock. By t=5 s, the entire flock is moving in a new direction opposite to that of the initial direction. More examples of collective turns are shown in Figs. S1 to S3 and Movies S1 to S3.

Figures 2, S4 and S5 shows the temporal variation of the group speed $U_g=|\boldsymbol{u}_g|$, radial acceleration $a_{ng}=|\boldsymbol{u}_g\times\boldsymbol{a}_g|/U_g$, turn radius $R_g={a_{ng}}^2/U_g$, turn rate $w_g=U_g/R_g$, polarization $\phi=|\langle\boldsymbol{u}/|\boldsymbol{u}|\rangle|$, and angular momentum $m=|\langle(\boldsymbol{x}-\boldsymbol{x}_g)\times\boldsymbol{u}/(|\boldsymbol{u}|\cdot|\boldsymbol{x}-\boldsymbol{x}_g|)\rangle|$. Here, the symbol $\langle\ \rangle$ implies an average over all individuals at one instant of time, and $\boldsymbol{x}_g=\langle\boldsymbol{x}\rangle$, $\boldsymbol{u}_g=\langle\boldsymbol{u}\rangle$, and $\boldsymbol{a}_g=\langle\boldsymbol{a}\rangle$ are the group centre, velocity, and acceleration

respectively. Since for all turns w_g increases to a peak w_g^{max} and then reduces (Fig. 2a; Fig. S4; Fig. S5), we define t_s as the time when w_g increases to $0.1w_g^{max}$ (approximately the time when a turn starts), t_m as the time when w_g reaches w_g^{max}, and t_e as the time when w_g decreases to $0.1w_g^{max}$ (approximately the time when a turn ends). The time for a group to complete a turn is thus $t_g=t_e-t_s$, and the change of traveling direction can be calculated as $\theta_g=\int_{ts}^{te} w_g dt$ (Table 1).

As t increases, U_g, R_g and ϕ decrease to minimum values near $t=t_m$ and then slowly recover (Fig. 2c, 2e, and 2i; Fig. S4; Fig. S5), while a_{ng} and m_g have the opposite trend (Fig. 2g; Fig. S4; Fig. S5). The increase of m and reduction of ϕ indicate that the flocks change from highly polarized motion to more of a milling state during the turn. For the case of $\theta_g\approx\pi$, the jackdaws with ranks $r_i=1$ and N move in opposite directions at $t=t_m$ such that their velocities nearly cancel and ϕ can be as low as 0.6 (Fig. 2j). The milling state is more apparent for larger θ_g (Fig. 2k).

Comparing turns with different θ_g, we find that w_g^{max} increases with θ_g (Fig. 2b) in such a way that all turns are completed in a nearly constant time (about 4 s) regardless of θ_g (Fig. 2l). The peak radial acceleration a_{ng}^{max}, however, remains nearly constant with increasing θ_g (about 7 m/s^2 or 70% of a jackdaw's body weight) (Fig. 2h). As a result, the minimum flight speed U_g^{min} decreases as $1/\theta_g$ (Fig. 2d), and the minimum group radius R_g^{min} decreases as $(1/\theta_g)^2$ (Fig. 2f). For the most extreme case, U_g^{min} is as low as 1.7 m/s and R_g^{min} is as low as 0.6 m.

(*b*) *Turn initiation locations within flocks*

To understand how information about the turns spreads between the birds and leads to a collective response, we investigated where turns are initiated in the flock. Figures 3(a-c), S6 and S7 show the spatial distributions of birds with $r_i<0.2N$ and $r_i>0.8N$ at $t=t_s$. We find that in transit flocks a turn can be initiated at the front of the flock, on the side, or even at the rear (Fig. 3a-b; Fig. S6). In contrast, in mobbing flocks, turns were always initiated at the front (Fig. 3c; Fig. S7). We define a vector $\boldsymbol{u}_s=\langle\boldsymbol{x}(r_i<0.2N;t=t_s)\rangle - \langle\boldsymbol{x}(r_i>0.8N;t=t_s)\rangle$ that points from the mean position of the birds with $r_i>0.8N$ to the mean position of the birds with $r_i<0.2N$, which gives the approximate direction antiparallel to the direction of information propagation. We calculate the angle between the two vectors $\boldsymbol{u}_s$ and $\boldsymbol{u}_g(t=t_s)$ (the group velocity at $t=t_s$), and denote it as θ_s. Thus, $\theta_s=0$ means that information propagates from front to back, $\theta_s=90$ degrees means that it propagates from side to side, and $\theta_s=180$ degrees from back to front. We find that for transit flocks θ_s varies from 0 to 180 degrees, while for mobbing flocks $\theta_s<60$ degrees (Fig. 3d; Table 1). We do not observe clear relationships between N and θ_s or between $\phi(t=t_s)$ and θ_s (Fig. S8).

We also find that in transit flocks the first birds that begin to turn can be located either near each other in a small volume or in totally different parts of the flocks (Fig. 3a-b; Fig. S6), while in mobbing flocks the initiators were always close to each other (Fig. 3c; Fig. S7). To quantify these tendencies, we computed V_{top}, the ratio of the volume occupied by the top ranked birds ($r_i<0.2N$) to the volume of the entire flock. To do this, we calculated the average distance between the furthest individuals for the selected top-ranked birds D_s and for the entire flock D at every time step. Then, we approximated $V_{top}=[D_s(t=t_s)/D(t=t_s)]^3$. We find that for transit flocks V_{top} varies from 0 to 1, while for mobbing flocks V_{top} remains very small (Fig. 3d; Table 1). We observed no clear relationships between N and V_{top} or between $\phi(t=t_s)$ and V_{top} (Fig. S8).

(*c*) *Information transfer speed in mobbing flocks*

For all mobbing flocks we observed, the birds that start to turn first are localized at the front of flocks and the turning information propagates gradually backward through the flocks (Fig. 4a; Fig. S9). Following a method used for starling flocks [21], we estimated the information transfer distance as $d_i=(r_iV/N)^{1/3}$, where $V=\langle\pi D^3/6\rangle_t$ is a measure of the time-averaged volume of the flock. Similar to starling flocks [21], we find regions during the turn where d_i increases linearly with t_i (Fig. 4b; Fig. S10), and the information

propagation speed c_s is obtained by fitting these linear regions. Attanasi *et al.* (2014) [21] first reported linear information propagation in the collective turns of starling flocks. They developed a theoretical model that included behavioural inertia of the birds and showed that this model can correctly reproduce linear propagation. A similar mechanism may be occurring here.

As N grows from 4 to 80, c_s initially increases and then becomes nearly constant (Fig. 4c; Table 1). In fish schools with group sizes ranging from 5 to 20, c_s was also found to increase with N [20]. The authors of that study proposed that this is because fish swim faster in larger groups. For jackdaws in mobbing flocks, however, bird flight speed is independent of N (Fig. S11). Studies of starling flocks found that c_s also increases with the polarization ϕ [21]. However, we find no clear relationship between the time-averaged group polarization $<\phi>_t$ and c_s (Fig. 4d), perhaps because of confounding effects due to group size. To isolate the effect of polarization on c_s, one would need to compare flocks with similar N, or flocks with N>30 where c_s is independent of N. Unfortunately, our current dataset does not have enough flocks with appropriate parameters to allow formal statistical analysis.

For the transit flocks, due to the large variation of V_{top} and θ_s (i.e., multiple initiation locations and various information propagation directions), the information transfer among birds is more complicated and cannot be modelled as a simple progressive information wave; thus, we did not attempt to estimate the information transfer speed for these transit flocks.

Discussion

In this study, we measured the collective turns of flocking jackdaws using a 3D imaging system. We obtained and analysed 21 collective turns for groups ranging from 4 to 196 individuals and directional changes of 100 to 240 degrees, taken from 13 transit flocks and 8 mobbing flocks. With these data, we can provide new insights on the collective turns of flocking birds.

We found first that jackdaws slow down during collective turns in both transit and mobbing flocks. Since fish also slow down during collective U-turns [20], this raises the possibility that this trend might be a common feature of collective movement in animals. There are several possible explanations for this phenomenon. The physics of animal locomotion, for example, imposes some constraints. Turning requires the production of a centripetal force, which increases with traveling speed. Flying or swimming animals generate these forces by pushing the surrounding fluid, and thus these forces are bounded. For birds, for example, the aerodynamic force is limited to a few times the body weight [52,53]. Thus, animals can make turns more easily by reducing their speed, which in turn requires a smaller centripetal force. Our results support this hypothesis, since the maximum centripetal forces we observe are about 0.7 times the body weight regardless of the magnitude of the change of traveling direction. A second possible reason, as suggested in the context of fish schools [20,51], is that lower speeds correspond to a less polarized group [68] and an increase of velocity fluctuations [51], driving the group close to a transition between aligned movement and a disorganized swarming state. Consequently, triggering collective turns may be easier at lower speeds [20,51].

We also found that the flocks complete their turns in a fixed amount of time regardless of the magnitude of the change of traveling direction. Switching to a new direction in a limited time might have significant benefits; for example, the flocks may be able to avoid predators more rapidly. To accomplish these equal-time turns, the flocks increase their turn rate, slow down more, and reduce the turn radius when changing their traveling direction more. Considering that both wingbeat frequency and mechanical power output increase as flight speed decreases for low flight speeds (<5 m/s) [69], jackdaws are likely to expend more energy when making sharper, lower speed collective turns.

Previous studies have shown that differences in behavioural and ecological context can affect group properties such as size, density, and polarization [5,7,70–72], as well as the interaction rules between

individuals [64,70]. Here, we find that context may also play a role in determining the locations where turns are initiated. In transit flocks, the first birds to turn can be located not only in the front and on the side of the flocks, but also in the rear. As a consequence, turning information can sometimes propagate from back to front. However, in mobbing flocks, the first birds to turn are always located at the front of the flocks. Results in transit flocks (Fig. 3a-b; Fig. S6) indicate that individual birds are able to respond quickly to neighbours located all around them. This ability may arise from jackdaws' wide field of vision, or perhaps from auditory cues as they are highly vocal during flight and can discriminate between the calls of different conspecifics [62,73]. The ability to initiate turns from any internal location also provides benefits to the flocks: given that predators may attack from different directions, all birds on the edges of the flocks can play a role in the detection of risk and trigger a collective response, which enables the flocks to detect risk faster and more effectively. This hypothesis may also explain why turns in mobbing flocks were always initiated from the front: in these cases, the birds are actively tracking the predator, and thus facing towards it as they circle overhead.

Additionally, the first birds to turn can be far apart from each other in transit flocks, unlike in mobbing flocks and previous studies of starling flocks where the initiators are always close to one another [21]. A possible explanation for this finding is that transit flocks contain multiple subgroups (Fig. S12), and each subgroup has a few individuals that have longer interaction range, so that they pay attention to environmental cues or birds at larger distances in addition to their local neighbours, and respond faster than other members. Indeed, our previous work has shown that jackdaw flocks in transit flights contain intermediate-range subgroups spread along the movement direction [38], and that there is variation in individual interaction ranges as jackdaws without social pair bonds interact with more neighbours than those with pair bonds [37]. It would be interesting to test whether our observations on the location of collective turn initiation hold for other animal groups that contain multiple subgroups [55] and have variations in individual local interaction rules [58].

Finally, we showed that the speed of information transfer increases with group size for small groups, but saturates for larger groups. This observation may be due to edge effects. As is evident from Fig. 4(b), birds with turning rank close to group size N (i.e., those on the flock edges) have longer time lags than birds in the centre of the flocks, perhaps because birds on the edges have to pay attention to the external environment in addition to their neighbours. When the group size is small, most birds are on the edges of the flocks, leading to a low information propagation speed. As the group size increases, the proportion of birds on the edges becomes smaller such that edge effects are weaker, and information propagation speed approaches a constant value. Note also that information propagation speed in large jackdaw flocks is about 7 m/s, much slower than the 15 to 30 m/s observed in starling flocks. This discrepancy might explain why individual jackdaw flocks become less ordered during collective turns (Fig. 2i), as jackdaws that turn later respond much slowly and thus have different flight directions as compared to those that turn first.

In conclusion, we have provided more observational data of collective turns of flocking birds. Our data help to better understand the turning kinematics and information transfer among birds. We also anticipate that kinematic and group size effects on information transfer we see will apply to other biological systems. Future studies, ideally with the capacity to trigger turns by using for instance simulated predator attacks, may help to illuminate what factors determine the locations of turn initiation, how these locations affect information transfer, and what interaction rules individuals obey during collective turns.

Authors' contributions

H.L., N.T.O., A.T., and R.T.V. conceived the ideas; G.E.M., J.W., and A.T. collected the data; H.L., N.T.O., K.V., and J.Y. analysed the data; all led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility
Data and code are available at: https://figshare.com/s/31aaa3454ec7f4b861b8

Ethical note
All field protocols were approved by the Biosciences Ethics Panel of the University of Exeter (ref 2017/2080) and adhered to the Association for the Study of Animal Behaviour Guidelines for the Treatment of Animals in Behavioural Research and Teaching.

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Competing interests
We declare we have no competing interests.

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Figures

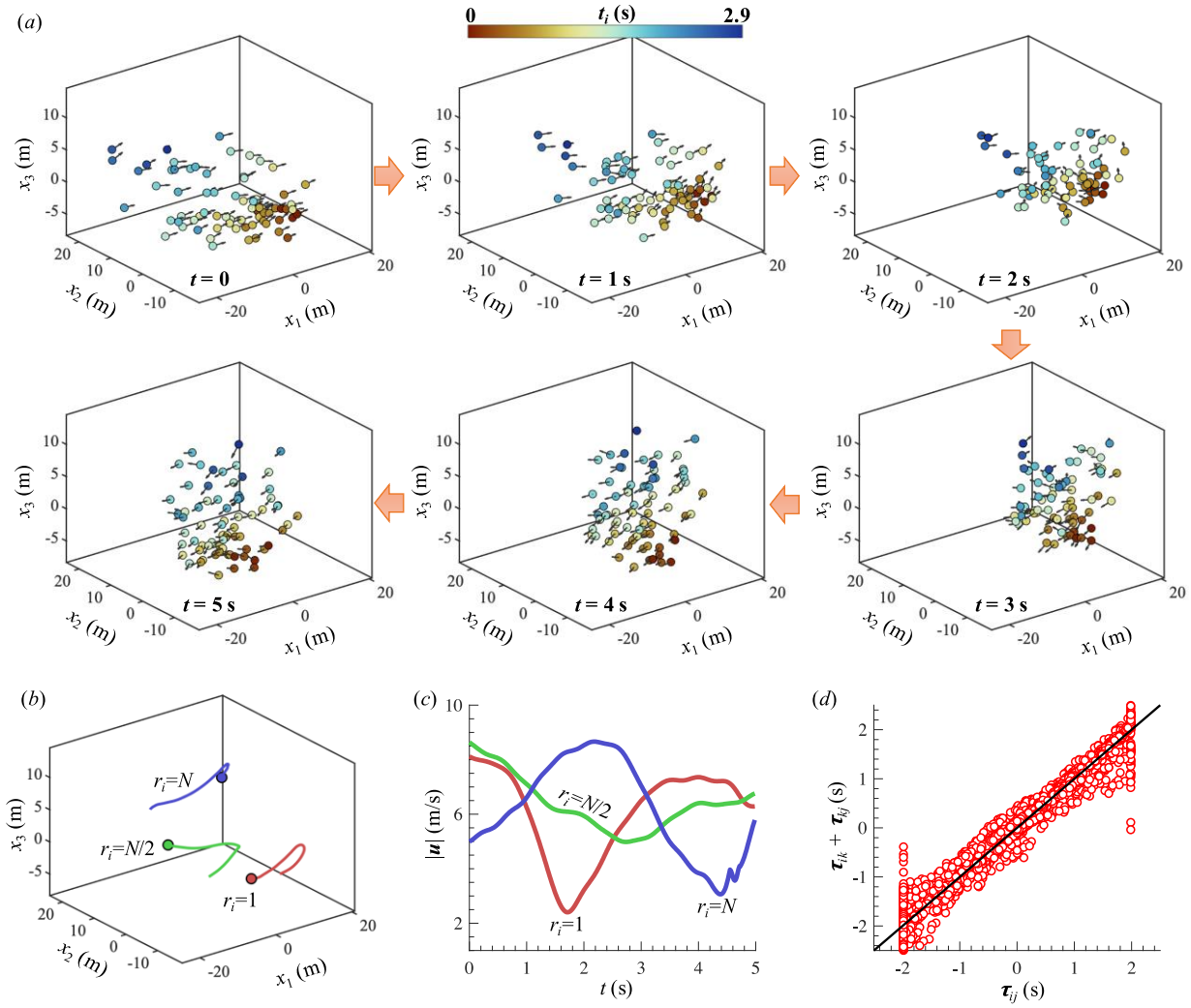

Figure 1. (*a*) Snapshots of positions (dots) and velocities (arrows) of individual birds in three-dimensional space during a collective turn made by flock #M05. Birds are coloured by the turning delay t_i. (*b-c*) Sample bird trajectories (*b*) and flight speeds $|\boldsymbol{u}|$ (*c*) for birds with turning rank r_j=1, *N*/2 and *N* taken from flock #M05 (dots are the ends of the trajectories). (*d*) Relation between τ_{ij} and $\tau_{ik}+\tau_{kj}$ showing that $\tau_{ij} \approx \tau_{ik}+\tau_{kj}$, indicating that the calculation of τ_{ij} is biologically meaningful. More examples of collective turns are shown in Figs. S1 to S3, and Movies S1 to S3.

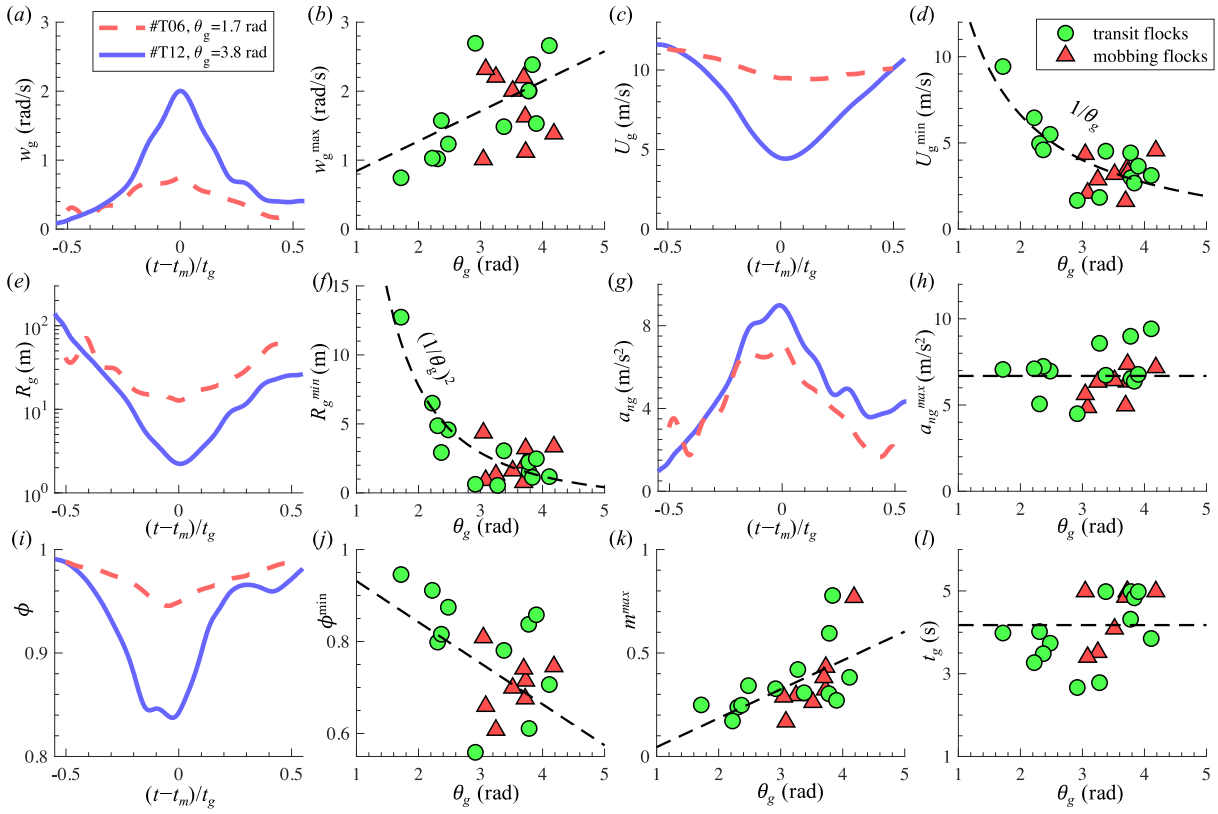

Figure 2. (*a*)(*c*)(*e*)(*g*)(*i*) Temporal variations of (*a*) group turn rate w_g, (*c*) group flight speed U_g, (*e*) group turn radius R_g, (*g*) group radial acceleration a_{ng}, and (*i*) group polarization ϕ during collective turns for flocks #T06 and #T12 (data for other flocks are shown in Figs. S4 and S5). (*b*)(*d*)(*f*)(*h*)(*j*)(*k*)(*l*) Effects of the magnitude of the change of traveling direction θ_g on (*b*) maximum group turn rate w_g^{max}, (*d*) minimum group flight speed U_g^{min}, (*f*) minimum group turn radius R_g^{min}, (*h*) peak group radial acceleration a_{ng}^{max}, (*j*) minimum group polarization ϕ^{min}, (*k*) maximum group angular momentum m^{max}, and (*l*) the time for flocks to complete turns t_g. Here, t_m is defined as the time when w_g reaches w_g^{max}.

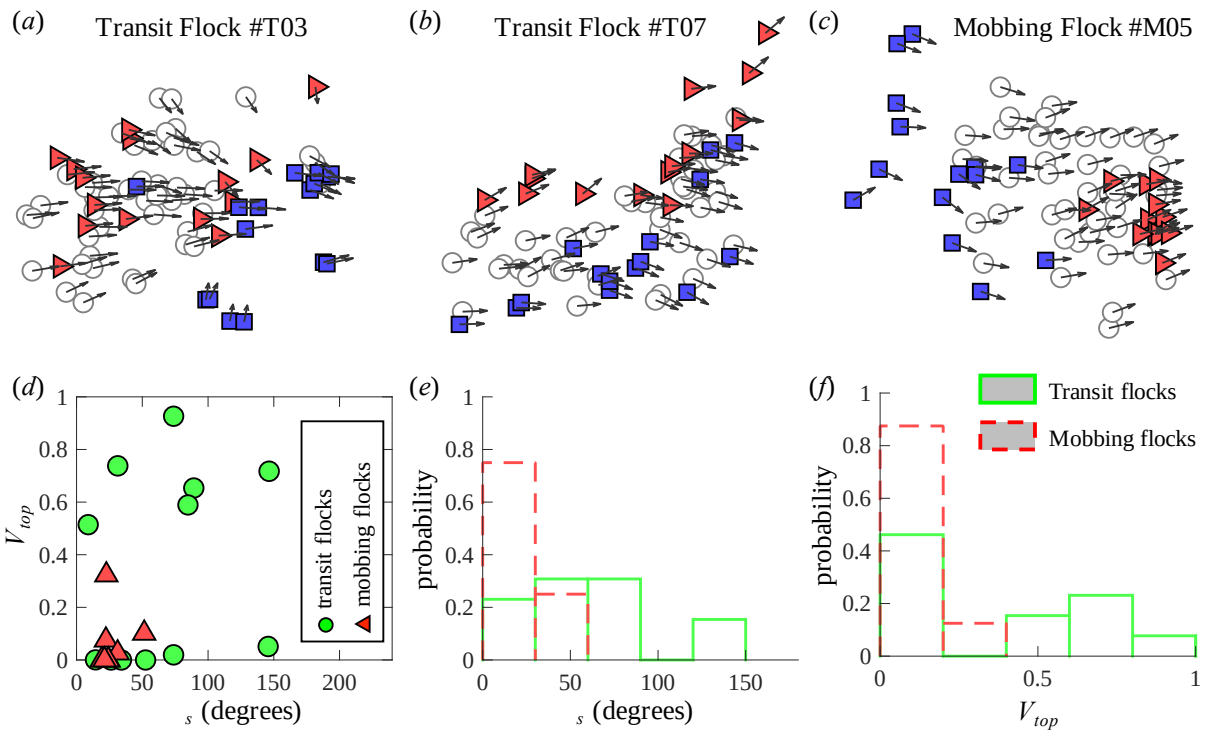

Figure 3. (*a-c*) Snapshots of positions (dots) and velocities (arrows) of individual birds projected onto a horizontal plane at $t=t_s$ (the time when a turn starts). Red triangles are birds with $r_i<0.2N$ and blue squares are birds with $r_i>0.8N$. Data for other flocks are shown in Figs. S6 and S7. (*d*) Distributions of θ_s and V_{top} for 13 transit and 8 mobbing flocks. (*e-f*) Probability density functions of (*e*) θ_s and (*f*) V_{top}. $\theta_s=0$ means that information propagates from front to back, $\theta_s=90$ degrees mean that it propagates from side to side, and $\theta_s=180$ degrees means that it propagates from back to front. Larger V_{top} means that the first birds that start to turn are further apart.

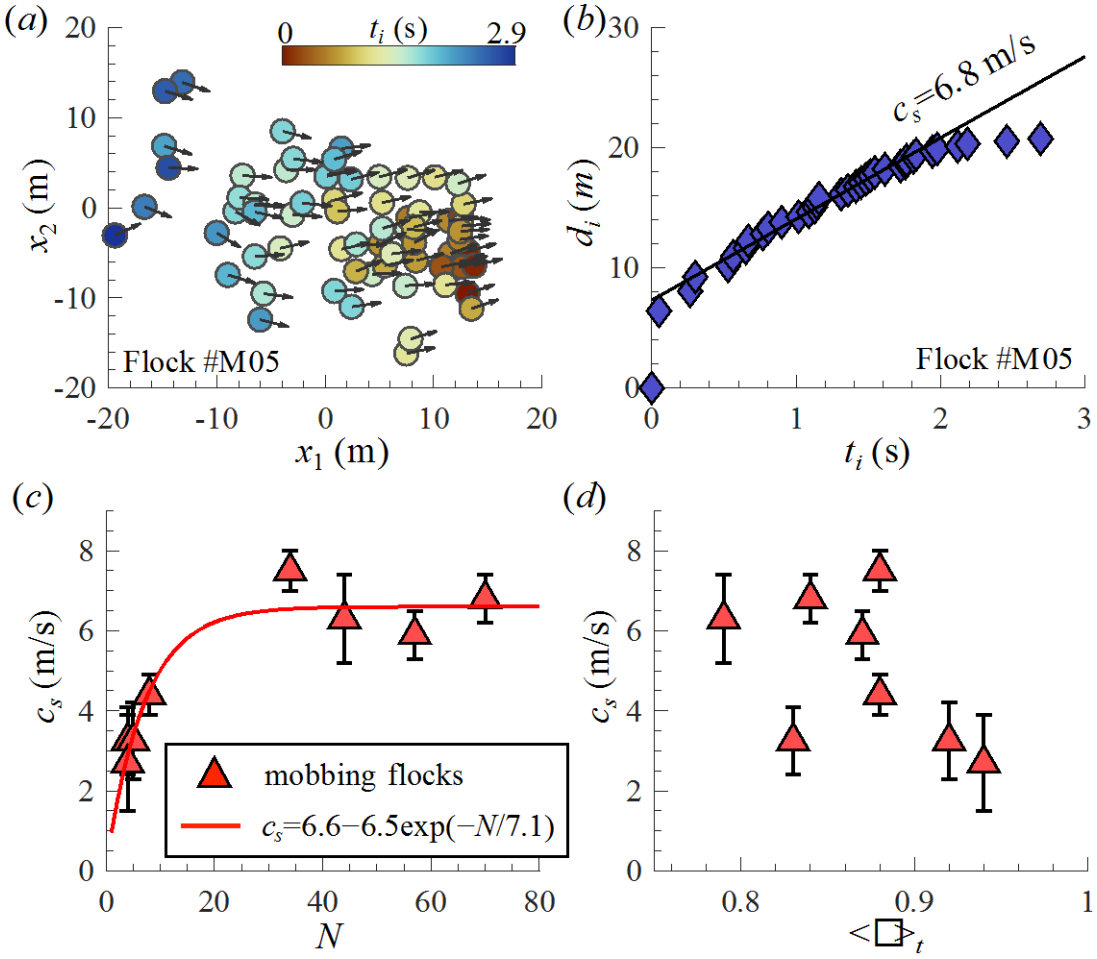

Figure 4. (*a*) Snapshots of positions (dots) and velocities (arrows) of individual birds projected onto a horizontal plane for flock #M05 at t=t_s (data for other flocks are shown in Fig. S9). Birds are coloured by t_i. (*b*) Information propagation distance d_i as a function of t_i for flock #M05 (data for other flocks are shown in Fig. S10). The information propagation speed c_s is obtained by fitting the linear region of the curve. (*c*-*d*) Relation between (*c*) N and c_s and (d) between time-averaged group polarization $<\phi>_t$ and c_s for the 8 mobbing flocks. Errors in c_s are due to the uncertainty when fitting $d_i(t_i)$.

Event	N	θ_g (*degrees*)	t_g (*s*)	$\phi(t=t_s)$	$U_g(t=t_s)$ (m/s)	θ_s (*degrees*)	V_{top}	c_s (m/s)
Transit flocks recorded during the winter seasons of 2018 and 2019								
T01	11	142	3.7	0.94	6.1	31	0.74	-
T02	15	132	4.0	0.99	10.1	14	0	-
T03	79	135	3.5	0.87	6.2	146	0.72	-
T04	196	235	3.8	0.72	9.7	74	0.93	-
T05	70	167	2.7	0.97	6.0	89	0.65	-
T06	25	98	4.0	0.99	11.3	146	0.05	-
T07	73	127	3.3	0.95	8.6	85	0.59	-
T08	6	217	5.0	0.95	9.7	26	0	-
T09	11	194	5.0	0.94	6.6	30	1	-
T10	4	220	4.8	0.90	10.5	52	0	-
T11	5	187	2.8	0.55	1.8	34	0	-
T12	19	216	4.3	0.98	11.1	73	0	-
T13	14	223	5.0	0.98	11.8	9	0.51	-
Mobbing flocks recorded between May and July of 2018								
M01	8	213	5.0	0.93	7.2	19	0	4.4
M02	4	239	5.0	0.95	7.5	24	0	3.3
M03	44	214	5.0	0.73	3.8	23	0.32	6.3
M04	57	201	4.1	0.93	6.8	22	0.07	5.9
M05	70	186	3.5	0.96	7.8	31	0.03	6.8
M06	5	212	4.9	0.88	6.8	24	0	3.2
M07	34	177	3.4	0.96	6.2	51	0.1	7.5
M08	4	175	5.0	0.93	6.0	21	0	2.7

Table 1. Statistics of 21 collective turns made by 13 transit flocks and 8 mobbing flocks. N is group size, θ_g is the change of traveling direction, t_g is the time for the group to complete the turn, $\phi(t=t_s)$ and $U_g(t=t_s)$ are the group polarization and speed at the beginning of the turn $t=t_s$, θ_s denotes the direction of information transfer through flocks (0 means from front to back, 90 degrees means from side to side, 180 degrees means from back to front), V_{top} denotes the volume ratio of the top ranked birds to the entire flock (larger values mean that the top ranked birds are farther apart), c_s denotes the information transfer speed.